GENETIC DIVERSITY IN RARE AND WIDESPREAD SPECIES OF *LOMATIUM* (APIACEAE)

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ABSTRACT

Levels of genetic diversity were assessed in populations of three rare species of *Lomatium* and three of their more widespread congeners. *Lomatium rollinsii*, *L. serpentinum*, and *L. laevigatum* maintain significantly less intrapopulational isozymic variation than do the more widespread *L. dissectum*, *L. grayi*, and *L. triternatum*. The limited genetic diversity of these rare species may result from genetic bottlenecks associated with their origins and/or genetic drift in small populations. The patterns reported here support the general trend reported for many other comparisons of rare and widespread congeneric plant species.

Assessment of the genetic diversity of rare plant species has become an important component of management programs for sensitive, threatened, and endangered species. However, despite several recent studies of genetic variation in rare and widespread congeners (reviewed in Karron 1987, 1991), no clear generalizations have emerged on the levels and patterns of genetic diversity in rare plant species (Karron 1991; Hamrick et al. 1991). For example, allozymic polymorphism is absent in several rare species (e.g., *Oenothera hookeri*, Levy and Levin 1975; *Chrysosplenium iowense*, Schwartz 1985; *Pedicularis furbishiae*, Waller et al., 1987; *Howellia aquatilis*, Lesica et al. 1988; *Bensoniella oregona*, Soltis et al. 1992; *Harperocallis flava*, Godt et al. 1997), but many other rare species maintain levels of polymorphism similar to or higher than those of their more widespread congeners (e.g., *Astragalus linifolius* and *A. osterhouti*, Karron et al. 1988; *Layia discoidea*, Gottlieb et al. 1985; *Aletes humulis*, Linhart and Premoli 1993; *Delphinium viridescens*, Richter et al. 1994, unpubl. data; several species of *Polygonella*, Lewis and Crawford 1995; *Achillea millefolium* ssp. *megacephala*, Purdy and Bayer 1996). Therefore, although most narrowly endemic plant species have low to moderate levels of genetic (i.e., allozymic) polymorphism (e.g., Pleasants and Wendel 1989; Les et al 1991; Bayer 1992; Sherman-Broyles et al. 1992; Baskauf et al. 1994; Cosner and Crawford 1994; Edwards and Wyatt 1994; Purdy et al. 1994; Purdy and Bayer 1995a, b; Godt et al. 1996; Wolf and Sinclair 1997; reviewed in Hamrick and Godt 1989 and Karron 1991), not all rare species are genetically depauperate. Furthermore, general trends in the levels and distribution of genetic variation may provide rough

MADROÑO, Vol. 44, No. 1, pp. 59–73, 1997

guidelines for the development of conservation and management strategies, but these guidelines may not be appropriate for all species (see review by Hamrick et al. 1991). Additional genetic studies of other rare species are therefore needed both to develop specific management programs and to improve our generalizations on the genetic structure of rare plant species.

Lomatium (Apiaceae) comprises 70–80 species of herbaceous perennials from western North America (Constance 1993). Of these, nearly half would generally be considered narrow endemics. Furthermore, many of these narrow endemics would be considered "geographically restricted" rare species (sensu Rabinowitz 1981; Rabinowitz et al. 1986; Karron 1991), occupying very limited ranges and comprising perhaps fewer than five known populations and 20,000 individuals. Because of the numerous rare species in *Lomatium*, and because species of *Lomatium* appear on the lists of sensitive, threatened, and endangered plant species of several western U.S. states, we assessed the levels and patterns of genetic diversity in three species with restricted distributions (*L. rollinsii* Math. & Const., *L. serpentinum* (M. E. Jones) Math., and *L. laevigatum* (Nutt.) Coult. & Rose) and compared these data with those for samples of three of their more widespread congeners (*L. triternatum* (Pursh) Coult. & Rose, *L. grayi* Coult. & Rose, and *L. dissectum* (Nutt.) Math. & Const.).

Lomatium rollinsii is restricted to fairly mesic areas in the meadow-steppe communities (Daubenmire 1970) of southeastern Washington and adjacent Idaho. It occurs only in Asotin County, WA, and Nez Perce County, ID. *Lomatium serpentinum* occurs on granite outcrops along the Snake River and its tributaries in Asotin County, WA, Nez Perce County, ID, and Wallowa County, OR. Given its apparent habitat specificity, *L. serpentinum* would also be classified as a "sparse" species (Rabinowitz, 1981). *Lomatium laevigatum* is narrowly distributed along the Columbia River in Klickitat County, WA, and Wasco County, OR. All populations occur within the Columbia River Canyon and fall within a 15-km strip along the river.

In contrast, *L. grayi*, *L. dissectum*, and *L. triternatum* have much broader distributions. *Lomatium dissectum* is perhaps the most widespread of all species of *Lomatium*, ranging from southern British Columbia and Alberta to southern California and Arizona and from near the Pacific Coast to Colorado. Three varieties have been recognized (Hitchcock and Cronquist 1973), but these intergrade considerably and are not consistently followed. *Lomatium grayi* ranges from northcentral Washington and northern Idaho south to northeastern Nevada and occasionally to southeastern Idaho, Wyoming, and Colorado. It is particularly common on rocky outcrops and in disturbed sites throughout southern and eastern Washington and in northcentral Oregon. *Lomatium triternatum* ranges from southern

Alberta and British Columbia to northern California, Utah, and Colorado and is particularly abundant in central and eastern Washington. *Lomatium triternatum* occurs in several habitats, including those supporting the meadow-steppe, sagebrush steppe, and ponderosa pine communities of the Inland Pacific Northwest (sensu Daubenmire and Daubenmire 1968; Daubenmire 1970). Morphological differences among populations in plant architecture, leaflet width, and fruit shape in particular have been recognized taxonomically at subspecific and varietal levels (Hitchcock and Cronquist 1973).

In this study, we examined levels of allozymic polymorphism in two or more populations of each of the rare and widespread species of *Lomatium* described above to see whether these rare species maintain lower, equivalent, or higher levels of genetic diversity than do their more widespread congeners. This information will be useful for any future management programs for the restricted species and will help to refine generalizations about the levels and patterns of genetic diversity in rare plant species.

Materials and Methods

Plant samples. Two populations each were sampled from *L. rollinsii*, *L. serpentinum*, and *L. dissectum*, along with three populations of *L. grayi*, four of *L. laevigatum*, and seven of *L. triternatum*. Collection data and sample sizes are given in Table 1. Leaves were collected from plants in the field, stored in plastic bags, transported to the lab on ice, and stored at −80°C until electrophoresis was conducted.

Electrophoresis. Electrophoretic protocols generally followed Soltis et al. (1983). Leaf samples were removed from the ultracold and were immediately prepared for electrophoresis by grinding in the Tris-HCl grinding buffer (Soltis et al. 1983) with 12% PVP. Fourteen enzymes were assayed, although not all enzymes were strongly expressed or clearly resolved in all species: aldolase (ALD), aspartate aminotransferase (AAT), fluorescent esterase (FE), fructose 1,6-diphosphatase (F1,6DP), glyceraldehyde 3-phosphate dehydrogenase (G3PDH), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), shikimate dehydrogenase (SkDH), superoxide dismutase (SOD), and triosephosphate isomerase (TPI). ALD, AAT, FE, LAP, PGI, SOD, and TPI were resolved on a modification (Haufler, 1985) of gel and electrode buffer system 8 (Soltis et al. 1983); IDH, MDH, PGM, 6PGD, and SkDH were resolved on buffer system 9 at pH 5.7; F1,6DP and G3PDH were resolved on buffer system 1. Staining for all enzymes followed Soltis et al. (1983), except that LAP was stained following Rieseberg and Soltis (1987).

TABLE 1. COLLECTION DATA FOR POPULATIONS OF RARE AND WIDESPREAD SPECIES OF *LOMATIUM* INCLUDED IN THIS STUDY. Sample sizes are in parentheses.

Rare species			
L. rollinsii	Washington:	Garfield Co.:	*Soltis & Soltis 2222* (32).
		Asotin Co.:	*Soltis & Soltis 2394* (12).
L. serpentinum	Washington:	Asotin Co.:	*Soltis & Soltis 2219* (8).
		Asotin Co.:	*Soltis & Soltis 2221* (46).
L. laevigatum	Washington:	Klickitat Co.:	*Soltis & Soltis 2189* (4).
		Klickitat Co.:	*Soltis & Soltis 2191* (18).
		Klickitat Co.:	*Soltis & Soltis 2192* (34).
	Oregon:	Wasco Co.:	*Soltis & Soltis 2209* (24).
Widespread species			
L. dissectum	Washington:	Whitman Co.:	*Soltis & Soltis 2257* (28).
		Whitman Co.:	*Soltis & Soltis 2311* (24).
L. grayi	Washington:	Whitman Co.:	*Soltis & Soltis 2312* (24).
		Whitman Co.:	*Soltis & Soltis 2414* (31).
		Whitman Co.:	*Soltis & Soltis s.n.* (Paradise) (27).
L. triternatum	Idaho:	Idaho Co.:	*Soltis & Soltis 2480* (32).
	Oregon:	Wheeler Co.:	*Campbell et al. 54* (32).
	Washington:	Asotin Co.:	*Soltis & Soltis 2485* (32).
		Kittitas Co.:	*Campbell et al. 62* (32).
		Lincoln Co.:	*Soltis & Soltis 2492* (32).
		Spokane Co.:	*Soltis & Soltis 2500* (32).
		Whitman Co.:	*Soltis & Soltis 2489* (32).

Genetic inference and data analysis. Regions of staining activity were numbered sequentially from the anodal portion of the gel, and allozymes were designated alphabetically from the most anodal allozyme in each staining region. Loci and alleles were inferred from the observed banding patterns and from the known subunit structure and subcellular compartmentalization of the enzymes (Gottlieb, 1982; Weeden and Wendel, 1989). For each population, we computed the proportion of loci that were polymorphic (*P*), the mean number of alleles per locus (*A*), and the mean (expected) heterozygosity (*H*).

Results

Twenty-five electrophoretic loci were interpreted, although not all loci could be scored for all populations: *Ald-1*, *Aat-1*, *Fe-1*, *Fe-2*, *F1,6dp-1*, *F1,6dp-2*, *G3pdh-1*, *G3pdh-2*, *Idh-1*, *Lap-1*, *Mdh-1*, *Mdh-2*, *Mdh-3*, *Pgi-2*, *Pgm-1*, *Pgm-2*, *Pgm-3*, *6pgd-1*, *6pgd-2*, *Skdh-1*, *Sod-1*, *Tpi-1*, *Tpi-2*, *Tpi-3*, and *Tpi-4*. *Pgi-1* could not be scored reliably in any population.

Rare species. Populations of *L. rollinsii*, *L. serpentinum*, and *L. laevigatum* maintain very low levels of allozymic polymorphism (Tables 2, 3). When the duplicated TPI loci with segregating variation (*Tpi-1/2* in *L. rollinsii* and *L. serpentinum* and *Tpi-3/4* in *L. laevigatum*) are excluded, the number of polymorphic loci is reduced even further. In *L. rollinsii*, only two of 13 loci were polymorphic in population 2222 ($P = 0.154$; Tables 2, 3), and only three of 14 loci were polymorphic in population 2394 ($P = 0.214$). In *L. serpentinum*, only *Pgi-2* (of 18 loci) was polymorphic in population 2221 ($P = 0.056$), and none of the 16 loci scored for population 2219 was polymorphic ($P = 0$). Three of the four populations of *L. laevigatum* (2189, 2191, and 2209) exhibited no allozymic polymorphism at any of the 19 loci examined whereas population 2192 had two polymorphic loci ($P = 0.105$). There were no fixed differences between populations in any of the three rare species, although slight interpopulational differences in allele frequencies were detected (Table 2).

Allelic diversity, as measured by *A*, and mean heterozygosity are also low in the three rare species (Table 3). Populations of *L. rollinsii* maintain slightly greater diversity than do those of either *L. serpentinum* or *L. laevigatum*. Values of *A* ranged from 1.14 to 1.31 (mean of 1.22) in *L. rollinsii*, from 1.0 to 1.06 (mean of 1.03) in *L. serpentinum*, and from 1.0 to 1.10 (mean of 1.02) in *L. laevigatum*. Expected heterozygosities ranged from 0.021 to 0.038 (mean of 0.030) in *L. rollinsii*, from 0 to 0.005 (mean of 0.002) in *L. serpentinum*, and from 0 to 0.030 (mean of 0.008) in *L. laevigatum*.

TABLE 2. ALLELE FREQUENCIES AT ELECTROPHORETIC LOCI IN POPULATIONS OF RARE AND WIDESPREAD SPECIES OF *LOMATIUM*. Note that not all populations could be scored for all loci; dashes indicate missing data. Allelic designations represent within-species variation; no attempt was made to compare alleles between species (see text). Allelic designations for *L. triternatum* are taken from a larger study of genetic structure in that species (Soltis et al., unpublished data); therefore, not all alleles are present in the seven populations included in this study. Asterisks indicate duplicated loci with tentative allelic designations (see text); these loci were not included in calculation of genetic diversity measures.

	Rare species population								Widespread species population											
	L. rollinsii		*L. serpentinum*		*L. laevigatum*				*L. dissectum*		*L. grayi*			*L. triternatum*						
Locus/Allele	2222	2394	2219	2221	2189	2191	2192	2209	2257	2311	2312	2414	Paradise	2480	2485	2489	2492	2500	54	62
Ald-1a	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Aat-1a	—	0.12	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	—	—	—	—
Aat-1b	—	0.88	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	—	—	—	—	—
Fe-1a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.0	0.0	0.35	—	—	—	—	—	—	—
Fe-1b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	1.00	0.65	—	—	—	—	—	—	—
Fe-2a	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	—	—	—	—	—	—	—
Fl,6dp-1a	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	—	—	1.00	1.00	—	0.0	0.0	0.0	0.07	0.0	0.0	0.0
Fl,6dp-1b	0.0	—	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.0	0.0	—	0.0	0.0	0.0	0.29	0.0	0.0	0.0
Fl,6dp-1c	0.0	—	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.0	0.0	—	1.00	1.00	1.00	0.64	1.00	1.00	1.00
Fl,6dp-2a	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	—	—	1.00	1.00	—	—	—	—	—	—	—	—
G3pdh-1a	—	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
G3pdh-2a	—	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	1.00	—	1.00	1.00	—
Idh-1a	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	1.00	1.00	1.00	—	—	—	—	—	—	—
Lap-1a	0.07	0.14	1.00	1.00	1.00	1.00	0.91	1.00	0.02	0.0	0.95	0.57	1.00	0.0	0.0	0.0	*	0.0	0.0	0.0
Lap-1b	0.88	0.86	0.0	0.0	0.0	0.0	0.09	0.0	0.15	0.32	0.05	0.09	0.0	0.02	0.0	0.02		0.02	0.03	0.0
Lap-1c	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.80	0.65	0.0	0.34	0.0	0.89	0.95	0.85		0.98	0.92	1.00
Lap-1d	0.03	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.02	0.0	0.0	0.0	0.09	0.03	0.02		0.0	0.05	0.0
Lap-1e	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.11		0.0	0.0	0.0
Mdh-1a	—	—	1.00	1.00	1.00	1.00	1.00	1.00	0.07	0.14	1.00	—	1.00	—	—	1.00	1.00	1.00	1.00	1.00
Mdh-1b	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.39	0.76	0.0	—	0.0	—	—	0.0	0.0	0.0	0.0	0.0

TABLE 2. CONTINUED

	Rare species population								Widespread species population											
	L. rollinsii		*L. serpentinum*		*L. laevigatum*				*L. dissectum*		*L. grayi*			*L. triternatum*						
Locus/Allele	2222	2394	2219	2221	2189	2191	2192	2209	2257	2311	2312	2414	Paradise	2480	2485	2489	2492	2500	54	62
Mdh-1c	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.54	0.10	0.0	—	0.0	—	—	0.0	0.0	0.0	0.0	0.0
Mdh-2a	—	—	1.00	1.00	1.00	1.00	1.00	1.00	—	—	1.00	1.00	1.00	—	—	0.97	—	—	1.00	1.00
Mdh-2b	—	—	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.0	0.0	0.0	—	—	0.03	—	—	0.0	0.0
Mdh-3a	1.00	1.00	—	—	1.00	1.00	1.00	1.00	—	—	—	—	—	0.0	0.0	0.18	0.02	0.0	0.0	0.0
Mdh-3b	0.0	0.0	—	—	0.0	0.0	0.0	0.0	—	—	—	—	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mdh-3c	0.0	0.0	—	—	0.0	0.0	0.0	0.0	—	—	—	—	—	1.00	1.00	0.82	0.95	0.87	1.00	0.77
Mdh-3d	0.0	0.0	—	—	0.0	0.0	0.0	0.0	—	—	—	—	—	0.0	0.0	0.0	0.03	0.0	0.0	0.0
Mdh-3e	0.0	0.0	—	—	0.0	0.0	0.0	0.0	—	—	—	—	—	0.0	0.0	0.0	0.0	0.13	0.0	0.23
Pgi-2a	0.97	1.00	1.00	0.05	0.0	0.0	0.28	0.0	—	—	0.0	0.03	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pgi-2b	0.03	0.0	0.0	0.95	1.00	1.00	0.72	1.00	—	—	0.0	0.24	—	0.03	0.50	0.0	0.0	0.0	0.04	0.0
Pgi-2c	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.96	0.40	—	0.0	0.0	0.06	0.0	0.0	0.0	0.0
Pgi-2d	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.04	0.32	—	0.97	0.43	0.90	0.90	1.00	0.82	1.00
Pgi-2e	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.0	0.0	—	0.0	0.03	0.03	0.10	0.0	0.0	0.0
Pgi-2f	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.0	0.0	—	0.0	0.03	0.0	0.0	0.0	0.14	0.0
Pgm-1a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	0.73	—	—	0.80	—	—	—	—	—	—	—
Pgm-1b	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	0.27	—	—	0.20	—	—	—	—	—	—	—
Pgm-2a	0.0	0.04	1.00	1.00	ab*	ab*	ab*	ab*	—	0.17	*	*	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pgm-2b	1.00	0.96	0.0	0.0					—	0.83				0.0	0.0	0.14	0.0	0.0	0.0	0.10
Pgm-2c	0.0	0.0	0.0	0.0					—	0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pgm-2d	0.0	0.0	0.0	0.0					—	0.0				0.77	0.90	0.84	0.50	0.68	0.71	0.79
Pgm-2e	0.0	0.0	0.0	0.0					—	0.0				0.23	0.10	0.02	0.47	0.32	0.29	0.11
Pgm-2f	0.0	0.0	0.0	0.0					—	0.0				0.0	0.0	0.0	0.03	0.0	0.0	0.0
6Pgd-1a	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	—	0.75	—	0.76	—	0.89	—	—
6Pgd-1b	0.0	—	0.0	0.0	0.0	0.0	0.0	0.0	—	0.0	0.0	0.0	—	0.25	—	0.24	—	0.11	—	—

TABLE 2. CONTINUED

	Rare species population								Widespread species population											
	L. rollinsii		*L. serpentinum*		*L. laevigatum*				*L. dissectum*		*L. grayi*			*L. triternatum*						
Locus/Allele	2222	2394	2219	2221	2189	2191	2192	2209	2257	2311	2312	2414	Paradise	2480	2485	2489	2492	2500	54	62
6Pgd-2a	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	—	0.15	—	*	—	*	—	*	*	*	*	—
6Pgd-2b	0.0	0.0	0.0	—	0.0	0.0	0.0	0.0	—	0.15	—		—		—					—
6Pgd-2c	0.0	0.0	0.0	—	0.0	0.0	0.0	0.0	—	0.69	—		—		—					—
Skdh-1a	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	—	0.10	—	—	—	—	—	—	—	—	—
Skdh-1b	—	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.90	—	—	—	—	—	—	—	—	—
Sod-1a	—	1.00	—	—	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	—	—	1.00	1.00	1.00	—	—
*Tpi-½**	abc	abc	abc	ac	*a/a*	*a/a*	*a/a*	*a/a*	*a/a*	*a/a*	*a/a*	*a/ab*	*a/a*	*	*	*	*	*	*	—
Tpi-3a	1.00	1.00	1.00	1.00	ab*	ab*	ab*	ab*	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	—
Tpi-3b	0.0	0.0	0.0	0.0					0.0	0.0	0.0	0.0	0.0	0.79	1.00	1.00	0.97	1.00	1.00	—
Tpi-3c	0.0	0.0	0.0	0.0					0.0	0.0	0.0	0.0	0.0	0.21	0.0	0.0	0.03	0.0	0.0	—

TABLE 3. GENETIC VARIABILITY MEASURES FOR POPULATIONS OF RARE AND WIDESPREAD SPECIES OF *LOMATIUM*.

Species/ Population	*P*	*A*	*H*
Rare species			
L. rollinsii			
2222	0.154	1.31	0.021
2394	0.214	1.14	0.038
Mean	0.184	1.22	0.030
L. serpentinum			
2219	0.0	1.0	0.0
2221	0.056	1.06	0.005
Mean	0.028	1.03	0.002
L. laevigatum			
2189	0.0	1.0	0.0
2191	0.0	1.0	0.0
2192	0.105	1.10	0.030
2209	0.0	1.0	0.0
Mean	0.026	1.02	0.008
Widespread species			
L. dissectum			
2257	0.222	1.56	0.096
2311	0.357	1.57	0.144
Mean	0.290	1.56	0.120
L. grayi			
2312	0.188	1.19	0.022
2414	0.133	1.33	0.081
Paradise	0.167	1.17	0.064
Mean	0.163	1.23	0.056
L. triternatum			
2480	0.556	1.67	0.146
2485	0.375	1.75	0.102
2489	0.462	1.77	0.109
2492	0.556	1.89	0.151
2500	0.333	1.33	0.075
54	0.273	1.45	0.079
62	0.222	1.33	0.079
Mean	0.397	1.60	0.106

Widespread species. Higher levels of polymorphism are maintained in populations of the more widespread species. In *L. dissectum*, population 2257 was scored for only nine loci, and two of these (*Lap* and *Mdh-1*) were polymorphic ($P = 0.222$). Population 2311 was polymorphic at five of 14 loci ($P = 0.357$): *Lap*, *Mdh-1*, *Pgm-1*, *Pgm-2*, and *6pgd-2*. In *L. grayi*, 15 loci were scored in population 2414, and 16 were scored in population 2312. *Lap* and *Pgi-2* were polymorphic in each, and *Skdh* was polymorphic in 2312 (and un-

scorable in 2414); *P* was 0.133 in population 2412 and 0.188 in population 2312. The Paradise population was polymorphic at two of 12 loci scored (*P* = 0.167): *Fe-1* and *Pgm-1*. In *L. triternatum*, *P* ranged from 0.273 to 0.462 (mean *P* = 0.356) in those three populations where 10 or more loci were scored and from 0.222 to 0.556 (mean *P* = 0.427) in the four populations where fewer than 10 loci were scored (Table 3). Furthermore, in a study of genetic diversity and population structure in 33 populations of *L. triternatum* (Soltis et al., unpublished data), levels of polymorphism ranged from 0.20 to 0.54 in those populations where at least 10 loci were scored and from 0.11 to 0.62 for those populations in which nine or fewer loci were scored. Mean values of *P* in the larger study were 0.389 for the 15 populations with 10 or more scorable loci and 0.420 for the 18 populations with nine or fewer scorable loci, with an overall mean of 0.406.

These more widespread species also maintain higher values of *A* and *H* than do the rare species (Table 3). Values of *A* ranged from 1.56 to 1.57 in *L. dissectum*, from 1.17 to 1.33 in *L. grayi*, and from 1.33 to 1.89 in *L. triternatum*. Mean values of *A* for *L. dissectum*, *L. grayi*, and *L. triternatum* were 1.56, 1.23, and 1.60, respectively. Values of *H* ranged from 0.096 to 0.144 in *L. dissectum*, from 0.022 to 0.081 in *L. grayi*, and from 0.075 to 0.151 in *L. triternatum*. Mean expected heterozygosities for populations of *L. dissectum*, *L. grayi*, and *L. triternatum* were 0.120, 0.056, and 0.106, respectively.

Discussion

Comparison of genetic diversity in rare and widespread congeners. The three rare species of *Lomatium* examined in this study have significantly lower levels of intrapopulational genetic diversity than do three of their more widespread congeners. Mean levels of polymorphism (*P*), allelic diversity (*A*), and expected heterozygosity (*H*) are all lower in the rare species than in the widespread ones even though only two populations of *L. dissectum* and three populations of *L. grayi* were examined. This pattern of reduced genetic diversity in the rare species is maintained when other genetic markers are used. Populations of *L. laevigatum* have identical chloroplast genomes (cpDNA) and DNA sequences from the internal transcribed spacers (ITS) of nuclear ribosomal DNA, whereas *L. grayi*, *L. dissectum*, and *L. triternatum* harbor both cpDNA and ITS variation (Soltis and Kuzoff, 1993; Soltis et al. unpublished data). This pattern also conforms to that observed in many other rare and widespread congeners (reviewed by Karron 1987, 1991), although populations of some rare plant species, such as *Layia discoidea* (*P* = 0.905; Gottlieb et al. 1985) and a population of *Polygonella robusta* (*P* = 0.727; Lewis and Crawford 1995), maintain very high levels

of genetic variation. Isozymic variation was not detected in several other rare plant species (e.g., *Oenothera hookeri*, Levy and Levin 1975; *Chrysosplenium iowense*, Schwartz 1985; *Howellia aquatilis*, Lesica et al. 1988; *Pedicularis furbishiae*, Waller et al. 1987; *Bensoniella oregona*, Soltis et al. 1992; *Lacondonia schismatica*, Coello et al. 1993), but most rare species examined to date maintain low to moderate levels of genetic diversity as measured by isozymes (e.g., species of *Coreopsis*, Cosner and Crawford 1994; Purdy et al. 1994; Purdy and Bayer 1995b; Hamrick and Godt 1989; Karron 1991).

Causes of reduced genetic diversity in rare species. As reviewed elsewhere (e.g., Karron 1991; Fiedler and Ahouse 1992), many factors may act singly or in concert to reduce levels of genetic diversity in rare species. For example, historical factors such as the age of the species and past changes in its distribution may affect the levels of genetic variation present both within and among populations of the species. A species of recent origin may have a restricted distribution and may maintain low levels of polymorphism because of a recent genetic bottleneck associated with speciation. Alternatively, a relictual species may have existed sufficiently long to accumulate mutations (see Lewis and Crawford 1995), but genetic bottlenecks may have reduced current levels of diversity. Furthermore, rare species of any age are particularly susceptible to stochastic changes in allele frequency (e.g., Wright 1931, 1938, 1956; Nei et al. 1975; reviewed in Barrett and Kohn 1991, and Ellstrand and Elam 1993) and to strong selection that may reduce levels of genetic diversity across populations of a species (e.g., Babble and Selander 1974) or eliminate rare alleles that are exposed in homozygotes that arise through increased inbreeding in small populations (e.g., Wright 1956). Furthermore, differences in life histories may contribute to differences in genetic diversity between rare and widespread congeners.

Which, if any, of these factors may be responsible, collectively or alone, for the reduced levels of intrapopulational allozymic diversity detected in rare species of *Lomatium* relative to their more widespread congeners? No apparent life-history characteristics differ between these rare and widespread *Lomatium* species, suggesting that differences in genetic diversity may more likely result from historical events and/or differences in population size. None of the three rare species appears to be of recent origin. A phylogenetic analysis of cpDNA restriction site variation in 30 species of *Lomatium*, representing all but one of the morphological groups in the genus (sensu L. Constance, personal communication), indicates that all three species are of more or less intermediate age (Soltis and Novak, 1996). Thus, genetic bottlenecks resulting from the *recent*

derivation of these rare species from more widespread and allelically diverse progenitors (sensu Gottlieb 1973, 1974) cannot be responsible for the limited genetic diversity detected in the narrow endemics. However, genetic bottlenecks could have accompanied their origins, but in the more distant past, and genetic drift in small populations is likely responsible for the maintenance of low levels of variation in these species.

Conclusions

Levels of intrapopulational genetic variation, as measured by isozymes, are significantly lower in rare species of *Lomatium* than in their more widespread congeners. This finding is similar to those reported for most other comparisons of intrapopulational genetic diversity in rare and widespread congeners. These additional data for species of *Lomatium* therefore support and strengthen the generalization that narrowly endemic plant species maintain only low levels of genetic variation. Furthermore, although only two (*L. rollinsii* and *L. serpentinum*) or four (*L. laevigatum*) populations of each rare species were sampled, only minor differences in allele frequencies were detected among populations. However, these populations may differ in attributes other than their isozyme profile (see Hamrick et al. 1991) and may be well adapted to their local environments. Possible genetic divergence in morphological, reproductive, and physiological traits, for example, should also be considered in the preparation of conservation and management strategies for all three species.

Acknowledgments

We thank Dan Crawford for helpful comments on the manuscript and Mary Jo Godt et al., Brett Purdy and Randy Bayer, and Paul Wolf and Robert Sinclair for permission to cite their unpublished manuscripts. This research was supported in part by NSF grant BSR-8918247 and NSF's Research Experiences for Undergraduates Program.

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